# THE BREEDING OF REEF ANIMALS

PART I. THE CORALS

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WITH SIX TEXT-FIGURES, ONE PLATE AND THREE TABLES

#### CONTENTS.

IAGE
. 219
. 220
. 235
. 241
. 242
. 243

# 1. PREFACE.

## (By T. A. STEPHENSON.)

ONE of our objectives during our residence at Low Isles was to discover, if possible, whether in a tropical marine area of this nature, the breeding of common animals goes on fairly steadily all the year round, or whether there is a concerted breeding season for the majority of them at some particular time of year. It may be stated at the outset that our work in this direction must be regarded as a preliminary study; it *does* provide a partial answer to the question just formulated; but it sketches in the details only slightly. It will be clear to anyone familiar with work of this nature that in dealing with a considerable number of species for one year only, in the intervals of other work, a complete picture could not be expected. The next workers to take the matter up, however, should now be in a position to carry it rapidly to a more advanced stage.

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21

DACE

The work on the gonads of corals was done by myself, both in the field and subsequently on preserved material; except that I have to thank S. M. Manton for carrying out the examination of the fresh gonads for me during two months of the year (27th April to 18th June, 1929). The work dealing with the liberation of planulae, however, was executed jointly, by S. M. Marshall and myself; and the majority of the collections and counts of planulae were made by her. In connection with this work we have to thank other members of the expedition, especially E. A. Fraser and A. P. Orr, for helping us with the collection of material. The text-figures, with the exception of Text-figs. 1 and 6, were drawn by Anne Stephenson, who also prepared some of the slides required. Other slides were made by F. C. Sherlock.

In the second part of this paper the results obtained with invertebrates other than corals will be described, by Anne Stephenson, who was responsible for that part of the investigation. The conclusions for the whole work together will there be stated.

# 2. THE GONADS OF CORALS.

## (By T. A. STEPHENSON.)

#### MATERIAL AND METHODS.

It was realized at the outset that the problem of breeding in corals can be attacked from two points of view. Since most of them are viviparous, one may attempt to discover their breeding season by finding out at what times they liberate planulae. On the other hand one may examine their gonads regularly, in order to find out when these are ripe. The latter method is less straightforward in the case of corals than it is in sea-urchins and certain other invertebrates whose gonads are relatively large and readily accessible, and in which the signs of maturity are comparatively easy to read. The polyps of a coral are often so small that a study of their gonads by any method other than that of cutting serial sections is impracticable; and even in the forms with large polyps, the examination of the gonads is a somewhat lengthy process. It was decided therefore to choose certain common forms with small polyps, and to discover if possible at what times these liberated planulae; and to choose other species with larger polyps for an examination of gonads. The choice of these latter forms was practically limited, at Low Isles, to three genera-Favia, Symphyllia, and Lobophyllia. It was also necessary to choose species which could be obtained from pools on the reef-flat or from shallow water on the seaward slope, otherwise the supply of material would have become too difficult. As it was, the supply began to run out by the end of the year, since no one species belonging to either of these genera was particularly plentiful. The form chosen as most suitable for the principal work was Favia doreyensis, a species which appeared to be as plentiful as any, and which (an important factor) can usually be recognized in the field without danger of confusing it with other species. Symphyllia recta was studied in lesser degree, and a few details were also observed for species of Lobophyllia. The latter, however, have in most cases to be obtained by diving; the number of species to be found is considerable, and they are not always easily distinguished from one another; and to obtain a regular supply of any one of them would have involved much more time than was available.

Several methods of examining the gonads of these corals were tried. In the case of Favia, it was found that the best way is to place a colony upside down on a board, and split it into several pieces, from below, with a cold chisel. (If the splitting is done from above it results in damage to a number of the polyps.) When possible, the colony may be split into radial slices similar to those into which one cuts a cake. If the splitting is successful, each of the cut surfaces presents the following picture : The proximal part of the colony is dead, but at a certain distance below the surface it becomes green in colour because of the presence of green filamentous algae which occupy the skeleton immediately below the living flesh of the polyps. The level at which the living tissue begins is therefore sharply marked by the cessation of the green coloration. Above the green region lies a neat row of longitudinally split corallites with their polyps, each as a rule displaying two mesenteries in surface view. The mesenteries cannot contract unduly because they are , attached to the skeleton; so the gonads and mesenterial filaments can be examined to advantage. The general examination was carried out under a binocular microscope, and a number of individual gonads in the fresh condition were removed from each colony for more detailed microscopic study.

Since each colony was cut into at least four, and usually six or more pieces, and since several polyps were exposed along each cut surface, the total number of gonads examined in any one colony was considerable. For instance, in an almost spherical colony whose diameter was 16 cm., and which was cut into halves, the number of vertical sections of polyps along each cut surface was 28; had this colony been divided into six equal radial pieces, the total number of such vertical sections would have been in the neighbourhood of 168; consequently the number of gonads to be seen in such a colony would have been anything up to 336. In another case the number of vertical sections exposed in six pieces which had been used for examination was counted, and amounted to 122; this would reveal a number of gonads not exceeding 244. The total number of colonies of Favia examined during the year was 230, and even if we take the average number of gonads examined in a colony as 100 (not a high estimate), this means that some 23,000 gonads altogether were studied. The examinations were carried out as nearly as possible at monthly intervals, though with some unavoidable irregularity. In the case of Symphyllia, which is harder to obtain, only 96 colonies were examined, and in that of Lobophyllia only 17. Colonies of Symphyllia were divided up in the same way as those of Favia; polyps of Lobophyllia were split up individually from below.

During the examinations a number of gonads were cut away from their mesenteries and fixed in Bouin's fluid for further study, and transferred after 24 hours to 70% alcohol. The preservation proved to be excellent. A number of whole polyps and portions of colonies were also preserved, some of these being fixed in neutral formalin and others in Bouin.

### THE OCCURRENCE AND RELATIONS OF THE GONADS IN CORALS.

The gonads of corals, like those of Actinians, are situated in the mesenteries, and constitute thickenings of these. They are to be found sometimes on all the mesenteries of any one polyp, sometimes on certain mesenteries only. Although there are a considerable number of details connected with them described in the coral literature (see p. 243), yet there is no great bulk of information concerning them in existence. The present report describes the first investigation, month by month, in the field : but still leaves many points unsettled.

In some species of colonial corals the sexes appear to be separate, whilst others are definitely hermaphrodite. In the hermaphrodite forms a single polyp may be male or female (at least at a given time), in which case it is the colony and not the individual which is hermaphrodite. In other cases each polyp is hermaphrodite, and when this is so, it may contain some mesenteries bearing ovaries alone and others which have only testes; or all the fertile mesenteries may be hermaphrodite. Where a mesentery includes both testes and ova, these may be arranged in distinct groups, or may be intermingled.

In a species with distinct sexes, the polyps on a given colony would be all male or all female. The case of *Pavona cactus*, recorded below, appears to be an example of this; and there are others. In examples of this kind, however, we cannot be certain that any species has separate sexes all its life, until we know enough about its life-cycle to be sure that it does not change its sex with age, or for other reasons.\* The condition of a colony at a given moment is not enough to establish its status, since even in hermaphrodite forms the gametes of one sex may develop before those of the other.

The general rule amongst corals appears to be viviparity, the fertilized egg developing into a larva before extrusion from the parent polyp; but there are also cases in which ova and spermatozoa have been extruded as such. Whilst some of the recorded instances may have been abnormal occurrences due to special conditions (planulae being present in the polyps at the same time), there is no reason to suppose that the extrusion of sperm at least is not perfectly normal in certain species. To what extent self-fertilization occurs in hermaphrodite forms we do not know. In the case of the viviparous forms a polyp may produce one planula at a time, or a number of larvae may reach the same stage together in a single polyp.

The position and structure of the gonads in some typical corals is illustrated by the figures accompanying this paper. To appreciate the relations of the various parts involved, it is necessary first of all to obtain a clear conception of the external features of a decalcified coral polyp, and several photographs are provided on Plate I which bring out the points at issue. In fig. 1 there are shown several living polyps belonging to a simply constructed coral (Euphyllia glabrescens). Here one sees, below the knobbed tentacles, which are only partly expanded, that portion of the column wall of the polyp (the edge-zone) which overlaps and extends down the outside of the skeletal cup. This edge-zone, in Euphyllia, is smooth, and has a sharply-defined lower margin, below which the rough and encrusted skeletal stalk is to be seen. In figs. 2 and 3 a single polyp of Lobophyllia, decalcified, is represented from two points of view-from underneath in fig. 2, more from the side in fig. 3. In this case the tentacles of the polyp are retracted and are therefore not visible; but the edge-zone is much in evidence, as a prominent saucer-like extension of the body. The spine-like processes which bound its upper margin are hollow extensions of the column-wall which fitted over actual spines in the skeleton, and are characteristic of the genus. Within the edge-zone is the conical body of the polyp, that part which occupied the skeletal cup during life. This conical portion is provided with deep longitudinal grooves, and into these the

\* A particularly interesting study of a large series of polyps of *Flabellum rubrum* is described by Gardiner (1902). The facts recorded appear to justify the conclusion that in this species the polyp is male when it first reaches sexual maturity, subsequently becomes hermaphrodite, and afterwards female; after the female phase it probably dies.

septa fitted before decalcification. At the apex of the cone is a sponge-like region consisting of membranous lamellae which occupied the interstices of the columella during life. The fertile portions of the mesenteries are contained in the lower parts of the ridges which intervene between the septal grooves. Fig. 4 shows a view. from underneath. of a larger polyp of Lobophyllia, which had two mouths and which had become slightly meandrine in shape: the effect of these modifications on the form and arrangement of its parts is demonstrated by the figure. The same process has been carried further in the fully meandrine species (Symphyllia recta) illustrated in fig. 5. Here a portion of a colony, instead of a single polyp, is represented, and the edge-zone, which is now limited to the margin of the colony, is not included in the part photographed. That part of the polyp which, in figs. 2 and 3, formed a simple cone, now has the aspect of a winding mountainrange separated by a deep valley from the corresponding part of the next polyp; but the furrows which originally contained the septa. and the ridges which contain the gonads, are plainly visible, although their arrangement is different. Lastly, in fig. 6 are seen the undersides of a number of decalcified polyps of Favia doreyensis. Here there is no meandriform modification. the simple individual polyps being united by a common sheet of tissue. In each polyp the grooves and ridges, the latter uniting centrally in an intracolumellar tangle of lamellae. are arranged as in Lobophyllia, though in this case the body of the polyp forms a pillar with a conical or more or less flattened lower end, instead of a simple cone as in Lobophyllia. Between the several polyps, the intermediate sheet of tissue which unites them is also grooved where it fitted, during life, over skeletal ridges.

The internal structure of the polyps of Favia doreyensis is illustrated in Text-figs. 1 to 5. Text-fig. 1 is an enlarged view of a single polyp divided vertically in half. The section passes on one side through one of the inter-septal alcoves which contain the mesenteries, and shows a mesentery with its gonad and mesenterial filament, and the relation of the intra-columellar tissue to the other parts; on the other side it passes through one of the fissures from which a septum has been dissolved away, and so reveals, in surface view, the wall of one of the inter-septal alcoves. Text-fig. 2 is a transverse section through the lower part of a similar polyp, and shows some of the central intra-columellar laminae, from which radiate alcoves of the coelenteron containing gonads and mesenterial filaments. It is noteworthy that the gonads in this part of the polyp are very bulky in proportion to the capacity of the coelenteron, and occupy a high proportion of the available space. The relation of parts in this section represents almost exactly the relations which obtain in a living polyp, since the body-wall in this region is firmly attached to the skeleton during life, and does not contract away from it during fixation, so that the natural proportion of the parts is preserved. Only that part of the polyp which lies above the skeleton, distal to the gonad region, can expand freely and so increase the size of the coelenteron; and in the species in question it does this only at night, remaining fully contracted in daylight. It will be further noted that in Text-fig. 2 no mesenteries are to be seen. This does not mean that they are absent, but that in this part of the polyp the bulk of the other organs is so great that they appear insignificant. and cannot be seen under a low magnification. Their presence, arranged in a typical manner, is shown in Text-fig. 3, which passes through a similar polyp distal to the fertile region. In Text-fig. 4 a single gonad is represented in detail. Here ova and testes are present, intermingled; and their finer structure is described on p. 229.



TEXT-FIG. 1.—Favia doreyensis. One half of a vertically divided decalcified polyp. The polyp is contracted, and the tentacles are, therefore, withdrawn, being concealed under the indrawn margin of the column. On the right side of the figure the cut passed through an exocoel, revealing an imperfect mesentery with gonad and mesenterial filament; the membranous covering of a small septum; and part of a perfect mesentery (attached to the throat) with its filament. On the left the cut passed through the fissure formerly occupied by a large septum, and thus reveals the wall of one of those alcoves of the coelenteron which lie between the septa. This figure should be compared with Text-figs. 2 and 3, and with the text, p. 223. In the gonad the eggs alone are represented, since the testes were too translucent to be accurately defined on this scale. A, throat (actinopharynx); CL, membranous lamellae of the columellar region; D, disc (peristome);  $E_N$ , a crest of the column wall bounding an endocoel, and previously occupied by a septum; Ex, a strip of the column wall bounding an exocoel; G, gonad; M, mouth; M1, imperfect mesentery; M2, perfect mesentery; MF1, the mesenterial filament belonging to the imperfect mesentery; MF2, the filament belonging to the perfect mesentery;  $M_{\mathcal{G}}$ , upper margin of column; PP, hollow process of the peristome which previously covered the paliform lobe of a septum; SA, the fold of body-wall which previously enclosed a small septum; SP, that part of the fold WA which covered the paliform lobe of a septum; T, tentacle; WA, one half of the fold of body-wall which covered a large septum; the cut edge of this fold is toothed where it followed the serrate outline of the septum.  $\times$  12.

## FAVIA DOREYENSIS.

FRESH MATERIAL.—The first of the 230 colonies examined were collected on 14th August. 1928. and the last on 18th June. 1929. There is thus a gap of two months in the year's record, but since it can be shown that this gap lies at the end of that part of the year during which the gonads were quiescent. it is probable that little more would have been discovered had it been bridged. The greatest diameters of the colonies used varied from 5.6 to 22.0 cm., the average being 13.7 cm. The majority were collected in the Western Moat, the others in adjacent parts of the Moat and in the Anchorage.\*

First of all it appears that, although the condition of the various gonads in a colony is not absolutely uniform, and in certain cases is somewhat variable, yet on the whole there is a fair degree of uniformity between them, so that as a rule the polyps of the whole colony are ripe or unripe together.

In the third week of August, six of the 26 colonies examined contained no gonads visible under a binocular. This means that although germ-cells may have been present in the mesenteries, they were in so undeveloped a condition as to make no appreciable swelling such as would be externally visible. In the other colonies gonads were visible; sometimes a few only could be seen, in other cases they were numerous; but in nearly all cases they were small and showed no signs of maturity. The gonads were from less than 1 mm. to 2 mm. in length, were colourless, pale green or pale blue, and contained a small number of immature ova. In one colony many of the gonads were larger than the rest and contained more eggs: and some of the eggs, usually the largest, were grey in colour instead of pale green.

In the second week in September, the 24 colonies examined showed no advance on those studied in August: in fact not one of the September colonies showed gonads as well developed as those of the colony mentioned at the end of the last paragraph, although immature eggs were usually recognizable. Colonies with no visible gonads were fewer than in August (3), but when gonads were present they varied in length from 0.5 to 2.25 mm. and were still very immature, pale green or blue-green in colour, and as before were few in number in some colonies and numerous in others.

Examination of 24 colonies towards the end of October and during the first two days of November still showed six colonies in which no gonads could be seen; but in the remainder the gonads were usually numerous or very numerous, and were in the main considerably more advanced than those examined in September. The colour of these gonads varied from pale green or blue-green to bright pale blue, greyish, or grey and green; the size from 1 to 3.2 mm.; and this time they were often relatively large and plump. The eggs were now frequently large, and were coloured quite definitely, opaque blue, purplishgrey, etc. Among the eggs were often to be seen smaller translucent sac-like testes, from some of which fully-formed active sperms could be extracted. The sperm has an acornshaped head, and a long tail. In other cases the testes were not sufficiently well developed to be demonstrable. This was the first time that the presence of testes in the gonads had been ascertained. In August and September none of them were seen, though they may have been present in an immature condition.

\* These localities are marked on the map of Low Isles given in Vol. III, No. 2, of these Reports, Plate I.



TEXT-FIG. 2.—Favia doregensis. Transverse section of a polyp, passing through the fertile region, and below the throat. The outline of the section is deeply indented by the fissures originally occupied by septa; and some of the lamellae of the columellar region are visible in the centre. The ova are black, their germinal vesicles white; the testes are stippled, and the mesenterial filaments, the bulk of which lie nearer the centre than the sex-cells, are shaded with strokes.  $\times$  31.



TEXT-FIG. 3.—Favia doregensis. Transverse section of a polyp passing through the throat and above the fertile region. There are 24 pairs of mesenteries, whose endocoels are occupied by folds of the body-wall which previously covered 24 septa. In the throat and mesenteries the mesogloea is black, the endoderm stippled and shaded with short strokes, the ectoderm shaded with long strokes; in the body-wall the whole thickness is represented in black, as the three layers are too thin to be treated individually.  $\times$  31.

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227

During the three days 29th November to 1st December, a further 24 colonies were examined. Five of these had no visible gonads; in the others the gonads were usually fairly or very plentiful. This time again the eggs were often large,\* and appeared to be very well developed, but were not readily liberated by the gonad—i. e. they did not float out of it as so often happens with the mature eggs of invertebrates. Their vesicular nuclei were usually clearly visible, even under the binocular, and the egg was crowded with small fluid spheres of perfectly regular form, which were completely free from one another. and streamed out of the egg if its membrane were ruptured (these details had been observed in earlier examinations also). The advance on the last month, however, seemed to lie mainly in the fact that in all the colonies which had gonads at all (save one) the presence of fully or almost fully formed, often active sperms was demonstrated; but the sperms did not readily leave the testes, and when motile were only moderately active. The condition of the gonads just described led to the supposition, on the anology of previous experience with other invertebrates, that although the gonads were maturing, they would not be ready for spawning for some little time. As the sequel will show, however, the spawning must have actually taken place during December, and perhaps also partly during November.

From the beginning of January onwards, until the middle of June, the results were entirely different. The number of colonies examined during these months was 132, and of these 99 had no visible gonads whatever. In the remaining 33 colonies there were present, usually in comparatively small numbers, very slight transparent or whitish patches or ridges on the mesenteries, occupying the proper position for gonads, and sometimes as much as 1 mm. or a little more in length (though commonly less), but very slender, and containing no recognizable eggs or sperms. In other words, there were the rudiments of gonads, containing more or less undifferentiated cells only. These undeveloped gonads were more plentiful in June than in any of the preceding months, suggesting that the corals were beginning to become sexually active once more, and would be ripening during the later months of the year, as was the case with those examined in the preceding year.

The indication of the facts recorded in the above paragraphs seems clear enough. Although the spawning was not actually witnessed, it appears evident that the gonads were ripening from August to the end of November, that spawning occurred in December (early summer), and that the gonads then died down into a rudimentary condition, or ceased to be externally visible on the mesenteries altogether, remaining in such condition until mid-June, when there were slight signs of renewed activity.

It will have been noted that even in the months during which the gonads of the great majority of the colonies were ripening, there were always a few colonies which showed no signs of sexual activity at all. Of the 98 colonies examined during the maturing period, 63 were more than 10 cm. in diameter, the remaining 35 measuring 10 cm. or less. Of the colonies larger than 10 cm., 48 had more or less *numerous* gonads, and only 4 had none at all; whereas of the colonies with diameters of 10 cm. or less, 16 had no visible gonads, and in the rest, although gonads were present, they were recorded as *numerous* only in 4 colonies. In the case of 18 colonies in which the gonads were either few or not very numerous, the average diameter was 10.7 cm., these forming an intermediate group with

<sup>\*</sup> Measurements of eggs preserved during these three days are as follows: Greatest diameter of ovum,  $305-374\mu$ ; greatest diameter of germinal vesicle,  $87-126\mu$ ; diameter of the principal nucleolus,  $17-37\mu$ .

some of its members on either side of the 10-cm. line. There is a distinct size-effect here, suggesting that on the average, colonies of this species begin to be strongly fertile only when their diameter has reached a figure in the neighbourhood of 10 cm.

It would also appear that a coral gonad advertises its maturity in a somewhat less distinct fashion than the gonad of many other invertebrates. In these latter one may expect the eggs to wash out more or less freely from a cut gonad when it is ripe, and may expect the sperms to show a very high degree of activity. The coral gonads never reached this condition so far as the recorded observations went.\*

PRESERVED MATERIAL.—Serial sections of a considerable number of isolated mature gonads were prepared. The stain used (iron haematoxylin) gave excellent results. In addition, series were made of two entire polyps, some of these being stained with haematoxylin and eosin, others with iron haematoxylin and light green.

The egg of Favia doreyensis (probably similar to that of many other corals) might make a very favourable subject for cytological study, because it is not only unusually large, but has also reasonably translucent contents. A typical mature egg of this species (Text-figs. 4 and 5) is spherical, subspherical or ovoid in shape, or is sometimes of less regular form. The cytoplasm is evenly packed with those spheres which were described above as characteristic of the living egg. The spheres themselves appear as cavities in the sections, but the cytoplasni between them stains lightly, and contains many small granules, probably of several kinds. Immediately below the surface of the egg there is a distinct cortical layer free from the above-mentioned spheres; and outside this a thin layer of mesogloea. The nucleus is large and vesicular, and lies at one side of the egg just below the surface, which it may slightly bulge outwards. One side of it is in contact with the cortical layer of the egg, or in cases where it lies just below the general level of the cortex, the latter dips inward a little to meet the nucleus. The nucleus contains a network dotted with fine strands and granules. It possesses a single large, spherical, eccentrically placed nucleolus, which is itself granular in structure. In addition to this there are several (3-6 in the cases counted) small subsidiary nucleolar bodies; and similar bodies sometimes occur in the cytoplasm just outside the nucleus, possibly representing material which has been extruded from the latter. The egg contains no zooxanthellae.

Testes, which are mixed up indiscriminately with the ova, lie sometimes peripheral to them and sometimes between them, tending to occur in groups, and are much smaller than the eggs. They consist of sacs of various shapes and sizes, containing numerous sperms. The tails of the sperms converge towards one end or one side of the sac, whilst their heads lie in radiating groups, and also occupy much of the peripheral part of the testis. In many gonads free sperms are to be found, which have escaped from their testes, and which lie between the ova. Since ruptured ova with the contents streaming out also occur, the liberation of these sperms from the testes may be entirely artificial. At the same time the testes are evidently in an easily ruptured condition.

The gonads whose structure has just been described were all preserved from 29th November to 1st December, 1928. The study of the fixed material supports the view already taken of the fresh, that the gonads were ripe or very nearly so at that time. Some further gonads, from a colony examined on 1st November, were also sectioned. These were in much the same condition as the ones preserved a month later.

\* Probably the eggs are dehisced through temporary openings in the endoderm of the gonad; but this was not actually seen,



TEXT-FIG. 4.—Favia doregensis. Section of a mature gonad, fixed on 30th November, 1928, passing through five ova and several testes. The section cuts the nuclei of two of the eggs, and these nuclei come in contact with the egg-cortex in other sections of the series, as in Text-fig. 5, B. The heads of the sperms are represented by dots, but they are shown as being less numerous than in reality, for the sake of clearness. Some of the testes have ruptured, and sperms have escaped into the tissue-spaces. The tissue of the gonad is in a reduced condition.  $\times$  ca. 170. Slightly diagrammatic,



TEXT-FIG. 5.—A, Symphyllia recta; B, Favia doreyensis. An egg of each species, the two represented to the same scale (× over 300). The details of egg-structure are described in the text, pp. 229 and 233. The figures are slightly diagrammatic.

## SYMPHYLLIA RECTA.

FRESH MATERIAL.—In the case of this species it was only possible to examine 96 colonies, at the rate of 12 a month, for 8 months. These colonies were obtained mostly from the Anchorage, a few from the Western Moat. Their average size (greatest diameter) was 18.5 cm., the smallest colony measuring 8.1 and the largest 28.0 cm.

As in the case of *Favia doreyensis*, a proportion of the colonies possessed no visible gonads at all; but of such colonies there were only 28, the remaining 68 having at least some trace of gonads.

In August only one of the 12 colonies examined had any trace of gonads; and in that colony only a single distinctly formed gonad could be found, this containing a few immature ova.

In October seven of the 12 colonies showed at least some signs of activity. In one of these, only a single small gonad with indeterminate content could be seen; in three other colonies young ova were found, but were present in very few mesenteries. In the remaining three colonies the gonads were better developed and fairly numerous, but had no decided colour. In the first of these colonies there were numerous eggs of various shapes and sizes, the larger ones measuring  $240-415\mu$  in diameter (when very slightly crushed by a cover-slip). Most of these eggs were translucent, and the nucleus was sometimes visible; but one was larger and opaque salmon in colour. Immature testes were probably present. In the second colony some of the gonads consisted of two quite distinct packets of eggs, one packet containing young colourless ova, the other containing much larger opaque salmon ones, well rounded and apparently mature, each with a translucent nucleus. In the third colony there were young ova, but very few of the larger salmon-coloured ones. In no colony were sperms identified.

In December the gonads of 12 further colonies were either absent or present in a rudimentary condition, the content being undifferentiated. Such gonads appear as slight translucent whitish spots or thickenings on the mesenteries, varying from 0.5 to 2.2 mm. in length.

During January, February, March and April, 48 colonies were examined. Only three of these were in so reduced a condition that no traces of gonads could be found; but in the rest, although there was at least some slight indication of gonads, only in two cases were these sufficiently well developed to contain determinate ova. The rudimentary gonads were often numerous. No testes or sperms were seen.

In May a slight increase of activity was observed, since in this month six of the colonies had yellow or yellowish-white gonads in which ova were present; and in one colony there were probably immature testes also. The gonads were fairly numerous in two of these colonies.

This scanty record provides little basis for any conclusion. So far as it goes, it appears to show that from December to April the gonads are in a quiescent condition. Signs of activity were found in October, possibly pointing to a spawning period in November, which would be close to that of *Favia doreyensis*. On the other hand there were formed gonads to be found in May also.

PRESERVED MATERIAL.—Serial sections of several gonads were cut, taken from a colony examined on 28th March, 1929; and in which ova of various sizes had been demonstrable in the fresh condition, the gonads being numerous and pale salmon in colour.

These sections, stained as before with iron haematoxylin, show a variety of ova which, though not as large as those of a mature Favia or Symphyllia, are nevertheless of considerable size (Text-fig. 5). The greatest diameter of the larger ones measured varies from  $188-335\mu$ : the diameters of their nuclei from  $54-100\mu$ : of their nucleoli from  $14-23\mu$ . The shape of the eggs varies considerably; they are often much larger in one diameter than in the other, and may be of curious forms, possessing processes which make their outline irregular. The germinal vesicle is large, usually with well-defined and deeplystained strands of chromatin. The nucleolus is large and spherical, and contains a clearly visible internal network in which there is sometimes a transparent vesicle. cytoplasm includes alveolar spheres, as in *Favia* ; and the substance occupying the intervals between them stains lightly, and includes a variety of fine granules with different staining properties. The spheres are somewhat smaller than in Favia. The surface of the egg is sometimes fairly well defined, sometimes less so. The superficial layers of the egg vary somewhat in appearance from one part of the egg to another. There is a cortical layer of variable depth, which has the character of an open network, contrasting with the darker, more solid-looking cortex of the Favia eggs. Below the cortex there is in some places a layer in which the alveolar spheres tend to be fewer. There occur in and somewhat below the cortex (and to a limited extent scattered through the cytoplasm) two kinds of unusually large and conspicuous granules. Some of these are stained grey, others black; or part of a granule may be grey and the rest black, suggesting that the two kinds of granule are phases of a single type. These granules may be very abundant in some parts of the circumference of the egg, scanty or absent in other parts, and typically the black ones form a conspicuous belt round one arc of the egg, being almost or completely absent from the opposite side. A similar arc of black granules may be found in some Favia eggs, but here they are smaller.

The state of affairs just described suggests, what would be expected on other grounds, that these eggs are less mature than the ones described under Favia, being in an earlier phase of their growth-period. No testes are to be distinguished in these gonads.

#### LOBOPHYLLIA.

FRESH MATERIAL.—In the case of *Lobophyllia* the data obtained are so few that they provide very little indication as to the time of the breeding season; besides which they apply to at least three distinct species. From the point of view of the structure of the coral gonad, however, they provide interesting information.

The 17 colonies examined were mostly obtained by diving, in or near the Anchorage. Three of them came from Batt Reef. Their greatest diameters varied from 10.7-22.0 cm. or more, the average being more than 16 cm.

The state of the gonads in these colonies was as follows :

(i) Eleven of the colonies, belonging to two species, were examined on 6-7th December, 1928. These either had no visible gonads at all, or else possessed rudimentary ones in which neither ova nor testes could be demonstrated, though in some cases the content was more differentiated than in others. Another colony examined on 9th February, 1929, had also rudimentary gonads.

(ii) One colony, examined on 2nd November, 1928, was heavily laden with eggs. which appeared to be well on the way to maturity, and had clearly visible nuclei. Their

diameters were of the order of  $270\mu$ . The gonads were salmon coloured, large and stout (5.0 to 8.6 mm. in length), but neither testes nor sperms could be found.

(iii) Another colony examined on the same date was in much the same condition as the one last mentioned, but in some of the gonads there was a small area (at the end of the gonad nearest the polyp's mouth) containing follicles which appeared to be immature testes.

(iv) A third colony examined on the same date was in a very interesting-condition. To begin with, numerous active sperms were extracted from it. whose structure could be clearly observed with the assistance of dark-ground illumination. The gonads usually contained both ova and testes, but sometimes testes only. Many of the eggs were large and salmon-coloured, often with the nucleus clearly visible. The riper testes consisted of bulky cream-coloured tissue, with a milky appearance. The relation between ova and testes varied considerably in different mesenteries; usually there were testes above and ova below; sometimes the two occurred intermingled. The testes occupied much more space than the ova, and apparently often included both ripe and unripe follicles. The shapes of the riper follicles were indistinct, and they appeared milky and contained numerous sperms; the shapes of the less mature follicles were more distinct, and these were translucent and colourless. Packets of immature follicles often occurred at the upper end of a gonad.

(v) A colony examined on 22nd October, 1928, had numerous large gonads, brownishsalmon in colour (5.0 to 5.5 mm. in length), which were universally distributed in the colony. The larger ova measured  $350\mu$ , etc., in diameter (slightly crushed by cover-slip). There usually occurred, above or beside the upper part of the ovary, a packet or packets of tissue of different texture, sharply marked off from the riper portion of the ovary. This tissue sometimes contained much younger eggs, but appeared in most cases to consist of immature testes. The presence of sperm in this case could not be certainly ascertained.

(vi) It will be noted that the four colonies just described were all in a more or less mature condition in late October or early November. The only other colony examined which had well-developed gonads was studied on 24th August, 1928, and had large (4 mm.) salmon-yellow gonads containing ova of various sizes.

## PAVONA CACTUS.

On the early morning (about 5.30 a.m.) of 30th November, 1928, a large colony of this coral, situated in the Western Moat, was seen to be slowly emitting milky clouds into the water. Two separated pieces of the same colony, which had been removed from the main portion and mounted on cement blocks in an adjacent pool (in connection with a growth experiment) were doing the same. Samples of the milky clouds were collected and centrifuged, and were found to contain numerous active sperms.

A group of seven polyps from one of these colonies was cut into serial sections. All these polyps were fertile, and none contained ova. In all of them there were (a) groups of cells which appeared to be spermatogonia, (b) testes (or parts of testes) containing numerous formed spermatozoa, and (c) testes which were partly empty and which appeared to have shed some of their contents. If the empty appearance of these testes is not an artefact (which I think improbable), it seems to indicate that the polyps to which they belonged were some of those which had actually been emitting sperm at the time when they were fixed. The presence of numerous unshed sperms makes it evident that spawning was not finished, and the spermatogonia indicate a further crop of sperms yet to come. The spermatozoa appear to escape from the testes through temporary openings in the endoderm. The histological condition of these polyps is also curious; the tissues include very large numbers of gland-cells of several types, which, judging from their turgidity, must have been in an active state; and the coelenteron contains considerable quantities of a substance which seems to be coagulated fluid with an affinity for haematoxylin.

These facts make it probable that the colony in question was a male one; but without sectioning hundreds of polyps and following the history of the colony for a considerable period, it would be impossible to be certain. It is not impossible that the cells which I take to be spermatogonia might be oogonia; but as far as I am able to judge, this is not the case.

# 3. THE LIBERATION OF PLANULAE BY CORALS.

## (By S. M. MARSHALL and T. A. STEPHENSON.)

The species chosen for this work included four branched forms—Montipora ramosa, Acropora hebes, Psammocora gonagra, and Pocillopora bulbosa; together with two massive species, Porites haddoni and Favia (Goniastrea) pectinata. The general plan with these forms was to collect either whole colonies, or branches from a number of colonies, at regular intervals, and to count any planulae which these might liberate. In practice the treatment had to be varied according to circumstances. and much more work was done on Pocillopora and Porites than on the other species. The details are as follows.

## MONTIPORA RAMOSA ACROPORA HEBES, PSAMMOCORA GONAGRA AND FAVIA PECTINATA.

The collections of these species were all made in the principal moat at Low Isles (the stretch of moat starting at the Western Moat and passing through the Middle and Fungia Moats to the Madrepore Moat). They covered the period 13th August, 1928, to 20th June, 1929; but we could not make enough of them to enable us to draw any conclusion. Since, however, over 50 collections were made altogether, and since not a single planula was obtained from any of these species on any occasion, it seems to be worth recording the dates upon which the negative results were obtained, so that they may form a starting-point for further work. It is a possibility that, at least in the cases of *Montipora* and *Acropora*, the records were all negative because these corals had been sterile all their lives, and would only become fertile once, all together, at a particular time, after which they would die. Evidence was obtained (and will be presented elsewhere) suggesting that an extensive growth of certain species of coral will spring up in a suitable locality, flourish for a time, and die out somewhat abruptly. That such a growth may breed before its extinction has been supposed by other workers, for instance Gardiner (1902, p. 470), who expresses a belief that " the ripening of the generative organs of a large number of polyp colonies of the same species in a single locality or habitat, followed by the subsequent death of all these colonies, is a regular phenomenon, . . . ."

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The method followed, as a rule, in making collections of the branched forms, was to break off some branches from a colony and put them into a screw-topped jar of sea-water for transport to the island, samples from 12 different colonies of each species being taken in this way on each occasion. On arriving at the laboratory, the contents of each jar were placed in a separate finger-bowl of sea-water, so that, had any planulae been liberated, it would have been possible to tell which colonies had produced them. In the case of *Favia* entire small colonies were used. The collections made, therefore, represented a number of coral colonies in the neighbourhood of 600. The dates on which the collections were made were as follows :

Montipora ramosa.—1928: 13th August; 4th November; 11th December. 1929: 7th, 25th, and 31st January; 12th February; 12th and 24th March; 11th and 23rd April; 9th, 17th, and 22nd May; 7th and 19th June.

Acropora hebes.—1928: 24th August; 4th November; 12th December. 1929: 7th and 25th January; 12th February; 12th and 24th March; 11th and 23rd April; 9th and 22nd May; 7th and 19th June.

Psammocora gonagra.—1928: 24th August; 4th November; 11th December. 1929: 7th January; 12th February; 12th and 25th March; 11th and 24th April; 9th and 23rd May; 8th and 20th June.

Favia pectinata.—1929: 25th and 31st January; 13th February; 12th and 25th March; 12th and 24th April; 9th and 23rd May; 8th and 20th June.

#### PORITES HADDONI.

The development of the planulae of this species has been described in an earlier report (Vol. III, no. 3); and it was there mentioned (pp. 129 and 130) that we cannot be certain that all our *Porites* planulae belonged to the same species. Since the identification of *Porites* species in the field is probably impossible at the present time, and since the limits of specific variation within the genus are still a matter of personal opinion, it is very difficult to speak with any assurance. On the other hand our material all came from the principal moat, and presented no variation in general form or texture which need be taken as constituting a specific distinction. The planulae which were reared all developed in the same manner, and presented identical details of structure and arrangement of parts. In a genus such as *Porites*, one might expect that in the early stages, if anywhere, differences of a specific nature would be particularly apparent; we therefore assume for the present that we were dealing with one species only.

The first production of planulae by *Porites* was noticed by C. M. Yonge on 26th January, 1929, when a single colony in an aquarium produced several dozen of them overnight. Colonies brought in from the reef on that date were also producing them. From that time onwards material was collected every few days until 10th June. The longest gap between collections, during this period, was 12 days, and usually was much less, over 30 collections, including hundreds of colonies, being made. After 10th June only two further collections were made, on 4th and 22nd July respectively.

The colonies were collected in different parts of the principal moat (Western Moat, Middle Moat, and Fungia Moat), but no differences in production were observed as between these different localities, which are nothing more than the parts of a very large pool. The colonies were usually brought to the island in buckets, each bucket containing on an average 20 to 30 of them. The planulae were subsequently picked out and counted. Sometimes colonies were then isolated from one another, by putting each into a finger-bowl of clean sea-water and allowing them to stand overnight; so that the relative numbers of planulae which they were producing could be observed. In such cases it would usually be found that one or two of them would produce planulae in considerable numbers (100 or more), the remainder each liberating only 2 or 3, or a small number. The greatest number of planulae was always obtained from the water in which the corals were collected, suggesting that the disturbance due to their removal from the reef acted as a stimulus to the liberation of larvae.

The numbers of planulae counted on the various dates are represented graphically in Text-fig. 6. and listed in full in the table on p. 242. From these it will be seen that production remained fairly high from 26th January until 10th June; and that at the two July collections it was much lower. Even in June the maximum number of planulae was lower than previously. No collection made during the entire period produced a negative result, and until July the number of planulae obtained from one pail on any one day never fell as low as a hundred and rarely below five hundred.

From these data it is quite evident that massive Porites was actively breeding on the Low Isles reef during the period January to May, 1929; and that the production was apparently falling off during June and July. If we are right in concluding that all the planulae belong to one species, then there is no suggestion of lunar periodicity in this breeding season, which would appear to be a continuous one.

## POCILLOPORA BULBOSA.

In the case of this coral all the planulae certainly belonged to a single species.

The corals were collected, as in the case of Porites, in the several parts of the principal moat. The species is a branched one, and during each collection branches were broken from a number of colonies. Sometimes the branches from each colony were brought to the island in separate jars, and subsequently isolated in finger-bowls; in other cases they were brought in buckets, in which case branches from different colonies were mixed. When the samples were isolated it was sometimes found that all of them produced planulae; sometimes that none of them did so; and at other times that some did so and others did not. In certain instances a collection from one part of the moat would produce a different result from a collection made on the same day in another part. The number of collections made altogether was in the neighbourhood of 80, and represented hundreds of colonies. The planulae, as before, were counted.

It may be noted that the collection of branches seems to be a better way of obtaining planulae than the taking of tow-nettings close to the coral. A tow-netting taken on a day when Pocillopora was known to be fertile, right round the moat and only about a foot above the coral, produced no planulae at all; and in the regular tow-nettings taken by Russell and Colman planulae were never captured over the reef flat, and but rarely out at sea.

The record begins with 7 collections which were made from 24th August to 5th September, 1928. No planulae were liberated from any of the samples then obtained, 23§ ш. 8.

with the exception of about 20 which were produced on 30th to 31st August. Full moon was on the 31st.

After this we have only two records before December. On 16th September and 4th November no planulae were produced from our samples.

From 11th December, 1928, to 24th July, 1929, the record is fairly continuous. The longest gap between collections, during that time, was 16 days, and was usually much less, the collections sometimes covering several consecutive days.

The results of this work are represented graphically in Text-fig. 6, and listed in detail in the table on p. 243. From the figure it may be seen that—

(1) Planulae were not obtained at every collection, as in the case of *Porites*. As will appear later, the negative results in this instance are as important as the positive ones.

(2) Planulae were obtained at about the time of new moon in the months December, February, March and April. The number obtained over each of these periods was large (1500 upwards), except in March, when less than 100 were counted. Between each of these four spawning-periods there were periods during which collections produced no planulae at all. In other words, there is evidence here of discontinuous breeding, the breeding periods occurring at about the time of *new moon* in each of the months mentioned. There is, however, a gap in January, which we cannot adequately fill. We know that after the December breeding period, and again in the latter part of January, negative results were obtained from collections, and also that somewhat *after* the time of new moon in January a few planulae were obtained; but we were prevented from collecting at the time of the new moon itself, and cannot, therefore, certify a breeding season at that time. It is probable, however, that the few planulae collected on 19th January represented the tail end of such a period.

(3) In the months of July, 1929, and August, 1928, planulae were obtained at about the time of *full moon*. The numbers collected were quite small. Negative collections were made before and after the productive period in August, and before the productive period in July; and collections at about the time of new moon in July produced no planulae.

From the above data we think it fair to conclude that in all probability Pocillopora bulbosa breeds discontinuously; that during the months December to April (summer and the beginning of winter), its breeding periods occur at about the time of new moon; and that during the months July and August (winter) they occur at about the time of full moon. If this is the case, we should expect a transitional period between the two phases. Such a transition is actually demonstrable between the last of the new-moon breeding periods (April) and the first full-moon period (July). Breeding occurred at and for some time after new moon in May, and for some time before full moon in June; during the interval between these two periods, it died down less completely than usual, but the definitive breeding period in June was delayed almost until full moon. In fact, it is possible that breeding was actually continuous, even though less active, during this interval, since we have only one negative record between the May and June breeding peaks, occurring among collections which yielded planulae in small numbers. The collections were neither frequent enough nor large enough to make it possible to rely too much on a single negative result. It may also be noted that the peak of production in June was less high than in May. The period of the opposite transition, from full moon to new, would occur some time between August and December; but our records do not cover that period.





In Table I an attempt has been made to summarize the results of the collections in another way. For the purposes of this table each lunar month has been divided into eight approximately equal periods, the centre of each period corresponding to a phase of the moon (new moon, first quarter, etc., and the intermediate points). Opposite each such period is listed the number of collections made during that period ; and the collections are recorded simply as positive (planulae produced) or negative (no planulae produced). The year is divided into three parts according to the type of production taking place, and the data for the several months included in any one of these parts are added together. This table emphasizes the fact that from December to April production took place only at or soon after new moon, while from July to November it took place only at and just after full moon. In May and June, the transition months, planula production was almost continuous, the only blank periods occurring soon after full moon.

Moon.	Decembe	r to April.	May an	d June.	July to November.		
	+	_	+		+		
•	7	1	4	0	0	0	
D .	6	0	2	0	0	2	
D	4	2	3	0	0	1	
0	0	3	4	0	0	3	
0	0	4	4	0	6	0	
0	0	1	0	2	1	2	
D	0	1	0	1	0	1	
D	0	2	2	0	0	1	

TABLE I.—Summary of data for Pocillopora bulbosa.

If our conclusion is justified, we have here an example of lunar periodicity of a novel description. Cases are already on record, and their number is steadily increasing, of animals which breed in relation to some definite phase of the moon; but so far as we are aware this is the first example of a transition from one phase of the moon to another phase, at a different time of year. We are aware that our data are, by force of circumstances, less complete than is to be desired; but feel that at present they are open to no other interpretation than the one made.

Is there any explanation which will help to elucidate a transition of this nature? So far as we can see at present there is none. There is a coincidence between the occurrence in question and the state of the tides, since during the summer months the lowest ebbs occur at the time of *full moon* and *at night*, whereas during the winter (May to October) they occur at the time of *new moon* and *in daytime*; but whether there is any connection between the tidal cycle and the reproductive cycle of the coral it is impossible to tell. The whole question of the relationship of daylight, moonlight and other factors to the question of reproductive maturity is one which at present is developing rapidly, but which we do not propose to discuss at the moment.

# 4. SUMMARY.

1. The corals studied were Montipora ramosa, Acropora hebes, Psammocora gonagra, Pocillopora bulbosa, Porites haddoni, Favia (Goniastrea) pectinata, Favia doreyensis, Symphyllia recta, Pavona cactus and species of Lobophyllia.

2. The position and structure of the gonads is described in the cases of *Favia doreyensis*, *Symphyllia recta* and species of *Lobophyllia*, from both living and preserved material. *Favia doreyensis* is hermaphrodite; the same applies to at least one species of *Lobophyllia*, and probably also to *Symphyllia recta*.

3. In Favia doreyensis the ova and testes occur, intermingled, on the same mesentery. The mature eggs are large  $(305-374\mu$  in diameter), and occupy a considerable amount of space in the body of a fertile polyp (Text-fig. 2). The gonads are reduced to a more or less completely rudimentary condition during the non-breeding season, becoming bulky as they mature. The development of the testes seems to lag somewhat behind that of the ova as the gonad matures, but probably both eggs and sperms become ripe at about the same time. Apparently the colonies of this species first become strongly fertile, on the average, when their diameter reaches a figure in the neighbourhood of 10 cm.

4. From periodic examinations of the state of the gonads, it is concluded that the majority of colonies of *Favia doreyensis* spawn in early summer (December), after which the gonads become rudimentary and remain so for some months, beginning to mature again some time in June. The act of spawning, however, was not witnessed. In the cases of *Symphyllia* and *Lobophyllia* no definite conclusion can be drawn from the data obtained; but it is possible that they may have spawning periods close to that of *Favia doreyensis*.

5. A colony of *Pavona cactus* spawned in the Western Moat on 30th November, 1928, liberating clouds of sperms. Seven polyps belonging to this colony were sectioned; they were all male, and their condition is described on pp. 234–5.

6. The liberation of planulae was studied in *Montipora ramosa*, Acropora hebes, *Psammocora gonagra*, *Pocillopora bulbosa*, *Porites haddoni*, and *Favia pectinata*. Of these species, only *Pocillopora* and *Porites* produced any planulae whilst under observation, the details being as follows :

7. In massive *Porites* (the data probably all apply to *P. haddoni*) breeding was going on actively from January to May, 1929. It still continued during June and July, but less actively. There is no indication of lunar periodicity in this coral.

8. In the case of *Pocillopora bulbosa*, evidence is presented which appears to warrant the conclusion that this species breeds discontinuously; that its breeding seasons occur about the time of new moon in the months December to April (summer and early winter); but that during the months July and August (winter) they occur at about the time of full

moon. There is a transition period in May–June. This appears to be the first case on record of a transition in spawning from new moon at one time of year to full moon at another.

9. Among the corals studied, therefore, we have one case (*Favia doreyensis*) of a short breeding-season in early summer; another (*Porites haddoni*) of a long continuous season lasting from summer into winter; and a third (*Pocillopora bulbosa*) of discontinuous breeding continued over most (if not the whole) of the year, and exhibiting distinct lunar periodicity.

# 5. TABLES.

In the following tables the word "sample" usually means a whole colony in the case of Porites, a group of branches taken from a single colony in the case of Pocillopora. The number of planulae given in the last column represents the total number liberated by the material collected on the date opposite which the number is recorded. Actually, in the case of certain of these records, some of the planulae would be given off on the day of collection, others during the subsequent night and morning, or occasionally even later. In column 2 the letters used indicate the part of the principal moat from which the material came; F = Fungia Moat, Ma = Madrepore Moat, M = Middle Moat, W = Western Moat; B refers to the part of the moat opposite a low place in the rampart, at the junction of the Fungia and Madrepore Moats.

Date.	Locality.	Amount collected.	Number of colonies which produced planulae.	Number of planulae produced.	Date.	Locality.	Amount collected.	Number of colonies which produced planulae.	Number of planulae produced.
$\begin{array}{c} 1929.\\ Jan. 26\\ ,, 26\\ ,, 27\\ ,, 27\\ ,, 27\\ ,, 29\\ ,, 31\\ Feb. 1\\ ,, 3\\ ,, 5\\ ,, 8\\ ,, 14\\ ,, 21\\ Mar. 6\\ ,, 7\\ ,, 12\\ ,, 14\\ ,, 20\\ \end{array}$	W F W W, M M M W W M M M M, W	<pre>1 pail ca. 9 samples 1 colony 69 samples 1 pail ? 2 pails 2 ,, ? 29 samples 3 pails ? 12 colonies 3 pails 3 ,, 3 ,, 2 ,,</pre>	Many	$\begin{array}{c} 1100 \\ A \ few \\ Dozens \\ ca. 2000 \\ Hundreds \\ 1600 \\ A \ good \ crop \\ 1200 \\ 1200 \\ + \\ 4000 \\ 500 \\ + \\ Large \\ number \\ Many \\ 5000 \\ 800 \\ -900 \\ 3400 \\ 2100 \\ 1000 \\ 1350 \end{array}$	1929. Mar. 21 ,, 27 ,, 28 ,, 29 April 4 ,, 7 ,, 8 ,, 17 ,, 24 ,, 24 ,, 24 ,, 24 ,, 24 ,, 24 ,, 24 ,, 24 ,, 28 July 4 ,, 22	M, W W M M F, M F W, M M F M M, F F M F, M F, M F, M	3 pails 2 ,, 3 ,, 4 ,, 4 ,, 1 pail 16 colonies. 10 ,, 22 ,, 12 ,, 15 ,, 2 pails 2 ,, 12 colonies 6 pails $\frac{1}{2}$ pail $\frac{1}{2}$ ,,	14 12 9	$\begin{array}{c} 3600\\ ca, 1200\\ 2200\\ 1600\\ 1150\\ 2500\\ 1700\\ 119\\ 83\\ 780\\ 1100\\ 2500-3000\\ 600-700\\ 1700\\ ca, 2000\\ 250\\ 1050\\ 26\\ 17\end{array}$

TABLE II.—Production of planulae by Porites haddoni.

Date.	Locality.	Amount collected.	Number of colonies which produced planulae.	Number of planulae produced.	Date.	Locality.	Amount collected.	Number of colonics which produced planulae.	Number of planulae produced.
1928. Aug. 24 ,, 28 ,, 29 ,, 30 ,, 31 Sept. 3 ,, 16 Nov. 4 Dec. 11	W W (probably) W W (probably) W W F W W W W	12 samples ca. 3 samples 6 samples 6 ,, 6 ,, 6 ,, 12 samples 12 ,,	At least	$ \begin{array}{c} 0 \\ 0 \\ ca. 18 \\ 2 \\ 0 \\ 0 \\ 0 \\ ca. 123 \end{array} $	1929. Mar. 24 ,, 30 April 10 ,, 11 ,, 11 ,, 11 ,, 12 ,, 17 ,, 23 May 2 ,, 6 ,, 9	Ma Ma F Ma Ma, B W F F F F F F Ma, F	12 samples 1 pail 1 ,, 2 pails 2 ,, 12 samples 1 pail 1 ,, 12 samples 14 ,, 1 pail 1 ,,	- 7	$\begin{array}{c} 0\\ 0\\ 1450\\ 1361\\ 535\\ 69\\ 24\\ 8\\ 0\\ 150-200\\ 1000 \end{array}$
,, 12 ,, 13 ,, 14 ,, 16 ,, 20 ,, 23 1929. Jan. 7 ,, 19 ,, 20	W F Ma Ma Ma	12 ,, 12 ,, 24 ,, 25 samples 12 ,,	8 At least 8	$\begin{array}{c} ca.110\\ 70 \text{ at least}\\ 2549 +\\ \text{many not}\\ \text{counted}\\ 24\\ 0\\ 0\\ 0\\ \end{array}$	., 9 ,, 10 ,, 13 ,, 15 ,, 17 ,, 19 ,, 22 ,, 24 ,, 27 June 3 ,, 7 ,, 7 ,, 8 ,, 11	Ma B B B F, B Ma, B B B Ma, B Ma B B	12 samples 3 pails $\frac{1}{2}$ pail $\frac{1}{2}$ , $\frac{1}{2}$ , $\frac{1}{2}$ , 12 samples $\frac{1}{2}$ pail $\frac{1}{2}$ , $\frac{1}{2}$ , 1	12 2 1 3	340 5000 1000 2000 550 75 6 17 0 1 30 5 52 25
,, 23 ,, 25 ,, 26 ,, 31 Feb. 12 ,, 15 ,, 16 ,, 17 Mar. 6 ,, 10 ,, 11 ,, 11 ,, 12 ,, 13 ,, 22	Ma F W, M F Ma F F F	1 collection 12 samples 1 pail 1 pail 12 samples 1 pail 1 ,, 1 ,, 12 samples 1 pail 1 ,,	12	0 0 0 Hundreds probably over 1000 Hundreds Few Very few 0 27 0 47 0 2 0	,, 15 ,, 17 ,, 18 ,, 19 ,, 20 ,, 20 ,, 20 ,, 20 ,, 21 ,, 26 July 4 ,, 10 ,, 19 ,, 20 ,, 21 ,, 22 ,, 21 ,, 20 ,, 21 ,, 22 ,, 21 ,, 20 ,, 21 ,, 20 ,, 21 ,, 20 ,, 21 ,, 22 ,, 22 ,, 22 ,, 22 ,, 22 ,, 24 ,, 24	M, Ma M, B M, B M M, B F F, M M B M, W, B	$\frac{1}{2}$ ,, $\frac{1}{2}$ ,, 12 samples $\frac{3}{4}$ pail 12 samples 8 pails 9 samples $\frac{1}{2}$ pail $\frac{1}{2}$ ,, 1,, 1,, 1,, 1,, 1,, 6 pails 2,,	4 ca. 7 6	$26 \\ 128 \\ 830 \\ 6 \\ 525 \\ Numerous \\ > 4000 \\ Numerous \\ 0 \\ 0 \\ 0 \\ 0 \\ 2 \\ 1 \\ 54 \\ 28 \\ 21 \\ $

#### TABLE III.—Production of planulae by Pocillopora bulbosa.

# 6. REFERENCES.

#### 1. CORAL GONADS.

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122

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#### DESCRIPTION OF PLATE I.

(For more detailed descriptions of these figures, see the text, pp. 222-3.)

- FIG. 1.—*Euphyllia glabrescens*. A group of branches broken away from a hemispherical colony. Photo graphed during life, with the polyps half expanded. Slightly larger than natural size.
- FIGS. 2 and 3.—Lobophyllia corymbosa. Two views of a contracted, decalcified polyp; seen from below in fig. 2, more from the side in fig. 3. Fig.  $2 \times 1.7$ ; fig.  $3 \times 1.8$ .
- FIG. 4.—Lobophyllia sp. A single contracted, decalcified polyp, viewed from below.  $\times$  1.8.
- FIG. 5.—Symphyllia recta. Part of the central portion of a colony, decalcified and viewed from below.  $\times$  1.7.
- FIG. 6.—Favia doreyensis. Part of the central portion of a colony, decalcified and viewed from below.  $\times$  1.6.

The material photographed for this Plate was collected at Low Isles, with the exception of the specimen represented in fig. 1, which came from Batt Reef.

Brit. Mus. (Nat. Hist.).



Photographs by T. A. Stephenson.

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6 5